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# On the odontology of certain marine Odontoceti and their dentine and enamel structures

A. Keil and H. von Nolting

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(From the Dental Institute of the University of Giessen)

# Zur Odontologie einiger mariner Odontoceten und deren Dentin- und Schmelzstrukturen

Zoologische Beitraege 15/1 1-31 (1969)

# On the odontology of certain marine Odontoceti and their dentine and enamel structures

by Albert KEIL and Heinrich VON NOLTING

(with 28 illustrations)

Ms. entered February 10, 1968

The dentition of the Recent Toothed Whales (Sperm Whales and Dolphins) comprises "either numerous homodont and in exceptional cases heterodont teeth, or only isolated, sometimes pseudoheterodont teeth, while the remaining teeth remain concealed within the gums or fail to develop" (M. WEBER 1927). Since only one set of teeth appears, the toothed whales are monophyodont. Probably in



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all odontocetan families this single set of teeth is the persisting first dentition. This view has been supported recently for sperm whales by findings of the present author (A. KEIL 1966). 'Giant denticles' occurring among normal teeth on the sperm-whale mandible can be interpreted as vestiges of the second dentition. Also the occasional detection of enamel on sperm-whale teeth which were previously thought to be without enamel (OHSUMI et al. 1963) is consistent with this interpretation. The first dentition is usually considered more 'conservative'. It still exhibits the formation of enamel which is no longer present in the second dentition (for the canines of deer in this regard, see FRANKENBERGER 1953).

In whalebone whales, embryonic teeth may still appear and even form hard substance, but they remain rudimentary and are soon resorbed. The whalebone whales seem to be the most specialized with respect to adaptation for the marine biotope, and this includes the disappearance of all their teeth. Even among the Odontoceti the functional importance of the teeth is variable, leading to different degrees and extents of reduction. Sperm whales can be considered a transitional stage; the upper row of teeth still emerge in some individuals (Figure 1), but usually they remain impacted as stunted structures. While we are well informed regarding sperm whales and their dentition, there are no comparable

findings yet concerning many other Odontoceti and their dentition, or concerning the structure of the teeth and their enamel covering. The number of teeth varies in the order Odontoceti from two to more than two hundred. The reduced number of teeth seems to be connected with the type of feeding. Specialization for cephalopods is supposed to entail a reduction in the

**Figure 1. Reduced dentition on the upper jaw of a sperm whale. From a colour photograph by A. KEIL on Sao Miguel Island, The Azores.**

number of teeth, or poorly developed teeth. Thus, according to S.H. PRATER (1965), "Some toothed whales live on the giant cephalopods found in the greater depths of the ocean. In such forms the teeth are feebly developed and are present, as in the Sperm Whale, only in the lower jaw." SLIJPER (1962) refers to the development of Cuvier's Beaked Whales; their fossil species possessed respectively 23 and 19 teeth, while Recent Ziphiidae have only two, or four to eight. KIRINO (1956) confirmed four to eight teeth on the lower jaw of Berardius bairdii,

with the backward teeth often no longer emerging, but remaining impacted. In ziphoid whales, the dentition is usually restricted to one pair of teeth on the lower jaw (BOSCHMA 1951).

YABLOKOW (1958) attempted to classify toothed whales in three groups according to their dentition: 1. Cetaceans with a large number of small teeth, a well developed pulp cavity, and a thin layer of cementum and enamel, such as most Delphinidae; 2. Cetaceans with fewer and larger teeth which do not possess enamel in adults, having instead a thick layer of cementum and smaller pulp cavity (Physeter macrocephalus, Delphinapterus leucas, and possibly Orcinus orca); and 3. Cetaceans with fewer teeth of considerably different shape, with a thick enamel coating and 'cementum' replacing the pulp (e.g., Berardius bairdii). This classification is defensible, except that both Physeter and Orcinus do have some enamel. Orcinus teeth normally have enamel.

3

## Material and Method

The material studied comprised mainly thirteen individual teeth from eleven species (survey on p. 4). The teeth were stored dry and kindly supplied to us by the Whale Research Institute in Tokyo. With additional material from Orcinus orca and Phocaena phocaena (taken from a beached animal at Sylt in 1966) and Tursiops truncatus, morphological and histological comparisons

were possible. Sperm-whale teeth were obtained from the Azores.

The external shape of the teeth and the size of their pulp cavities were photographed and x-rayed. For ground thin sections, the material was sectioned with a water-cooled diamond disk and the sections were ground manually with grindstones of different grain until only first-order polarization colours appeared in the enamel (if enamel was present) or the section became transparent. The sections ranged from 15 to 80 µm in thickness. The embedding medium was Eukitt. Some sections were decollagenated (boiled in glycerol potassium hydroxide solution) for a polarizing microscopic analysis of their imbibition behavior. Also untreated sections were ~~imbibed~~ infiltrated with ~~in~~ liquids of different refractive indices to make it possible to evaluate the degree of mineralization of the enamel between crossed polars. The microscopic analysis took place with transmitted light, polarized light, and phase contrast.

Morphological classification of the teeth

Without exception, the teeth of the eleven species studied were conical, or haplodont. They varied greatly in size. The grouping of these teeth by shape, number, size, composition of the tooth hard substances, and size of the pulp cavity can be seen in Figures 2 to 14 and Table 1.

Table 1
Survey of teeth and species investigated

| Lfd. Nr. | Art | Körperlänge in m | Zahn- Form | Zahn- Zahl | Zahn- Größe in cm | Zahnhartsubstanzen | Pulpacavum |
|---|---|---|---|---|---|---|---|
| 1 | *Orcinus orca* (Schwertwal) | ++ 10 | ++ | +– 44 | ++ 8 | ++ | ++ |
| 2 | *Berardius bairdii* (Entenwal) | ++ 10 | –– | –– 4—8 | ++ 6,7 | +– | –– |
| 3 | *Ziphius cavirostris* (Gänseschnabelwal, Cuviers Spitzschnauzendelphin) | ++ 5 | ++ | –– 2 | ++ 4,4 | ++ | +– |
| 4 u. 6 | *Globicephala scammoni* ♀ (Grindwal) | ++ 4,43 | ++ | +– 40 | ++ 4 | ++ | –– |
| | *Gl. sc.* ♂ | +– 2,30 | ++ | +– 40 | +– 3,5 | ++ | ++ |
| 5 u. 7 | *Tursiops truncatus* ♀ (Großer Tümmler) | +– 3,06 | ++ | ++ 84 | +– 3,6 | ++ | +– |
| | *Tursiops truncatus* ♂ | +– 3,15 | ++ | ++ 84 | +– 2,7 | ++ | –– |
| 8 u. 10 | *Stenella caeruleoalba* (Blau-weißer Fleckendelphin) ♀ | +– 2,27 | +– | ++ 100 | –– 1,5 | ++ | ++ |
| | St. c.-a. ♂ | –– 1,37 | ++ | ++ 100 | –– 1,3 | ++ | ++ |
| 9 | *Lagenorhynchus obliquidens* (Streifendelphin) ♂ | –– 1,75 | ++ | ++ 118 | –– 1,5 | ++ | ++ |
| 11 | *Delphinus delphis* ♀ (gewöhnl. Delphin) | –– 1,84 | +– | ++ 200 | –– 1,3 | ++ | –– |
| 12 | *Phocaena phocaena* (Kleiner Tümmler) | –– 1,80 | –– | ++ 100 | –– 0,9 | ++ | +– |
| 13 | *Physeter macrocephalus* (Pottwal) | ++ 12—16 | ++ | +– 40—73 | ++ 12—16 | +– | +– |

Key: 1- serial no. 2- species 3- body length in m 4- shape of teeth 5- no. of teeth 6- size in cm 7- tooth hard substances 8- pulp cavity 9- Killer Whale 10- Baird's Whale 11- Cuvier's Beaked Whale 12- Pilot Whale 13- Bottle-nosed Dolphin 14- Blue-white Dolphin 15- Pacific White-sided Dolphin 16- Common Dolphin 17- Common Porpoise 18- Sperm Whale Symbols refer to the classification of the teeth on p. 7: a= + +; b= + –; c= – –. (See also p. 7.) 'u.'= 'and' Read commas as decimal points.

The teeth in Figure 2 are arranged according to size. Occasionally, when the size of the animals was not known from the material supplied, it was added from the literature (SLIJPER 1962, NORMAN, FRASER and SCHUBERT 1963).

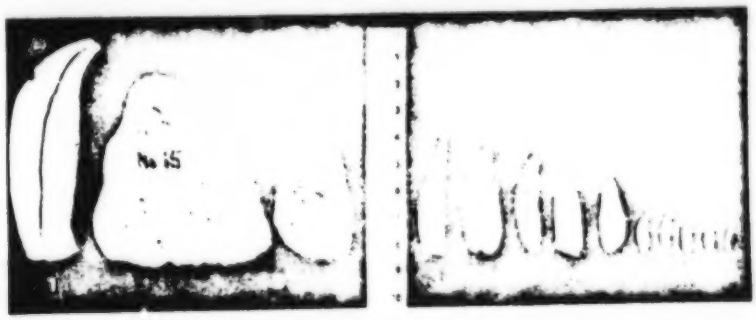

Figure 2. Teeth investigated from 11 species of the order Odontoceti (see also Table 1).

1. Classified according to specific type of conical shape, and frequency of occurrence: 5

a) The simplest, and at the same time the most common modification is an arcuate contour on one or both sides: Killer Whale (no. 1), Cuvier's Beaked Whale (no. 3), Pilot Whale (no. 4 and 6), Bottle-nosed Dolphin (no. 5 and 7), Pacific White-sided Dolphin (no. 9), and Blue-white Dolphin (no. 10).

b) Corkscrew shape (added bending of the root): Blue-white Dolphin (no. 8) and Common Dolphin (no. 11).

c) Lanceolate to spatular shape: Common Porpoise (no. 12), and triangular shape: Baird's Whale (no. 2).

2. ...according to number:

a) 100 or more: Bottle-nosed Dolphin (no. 5 and 7), Common Porpoise (no. 12), Common Dolphin (no. 11),

and Blue-white and Pacific White-sided Dolphins (no. 8, 9, and 10).

3. ...according to size:

a) 4 - 10 cm: Killer Whale (no. 1), Baird's Whale (no. 2), Cuvier's Beaked Whale (no. 3), and Pilot Whale (no. 4); over 10 cm: Sperm Whale (no. 13).

b) 2 - 4 cm: Bottle-nosed Dolphin (no. 5 and 7) and Pilot Whale (no. 6).

c) up to 2 cm: Common and Pacific White-sided Dolphins (no. 9 and 11), Blue-white Dolphin (no. 8 and 10), and Common Porpoise (no. 12).

4. Presence of tooth hard substances:

Enamel, dentine, and cementum were present in all teeth investigated except the unenameled tooth of Baird's Whale (no. 2).

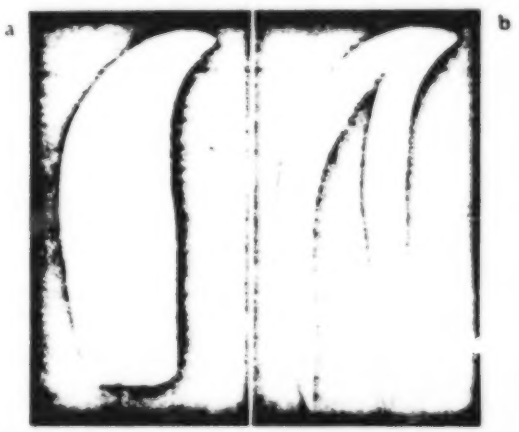


Figure 3. Orcinus orca, Killer Whale tooth; a) lateral aspect, b) x-ray of a ground thin section from the middle of the tooth. Note the strongly calcified, and therefore less radiolucent, enamel cap. Size reduced 2:3. (b from A. KEIL 1966)

5. Presence and size of pulp cavity: 6

a) taurodont (with large pulp): Killer Whale, Pilot Whale, Pacific White-sided Dolphin and Blue-white Dolphin.

b) Cynodont (with small pulp): Cuvier's Beaked Whale, Pilot Whale, Bottle-nosed Dolphin, Blue-white Dolphin, and Common Porpoise.

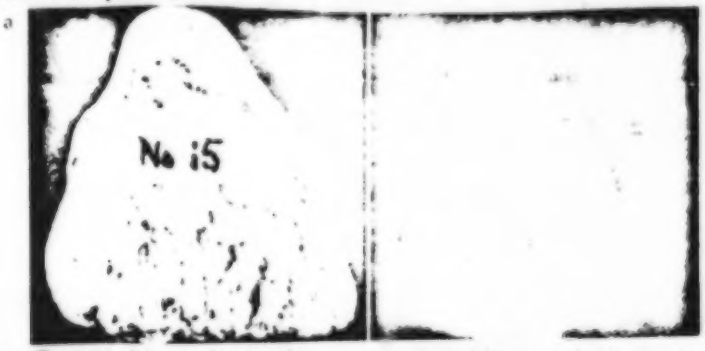


Figure 4. Berardius bairdii, a) tooth in lateral aspect, b) x-ray. Size reduced 3:4.

c) 'Lithodont' (pulp obliterated): Bottle-nosed Dolphin, Common Dolphin, and Baird's Whale.

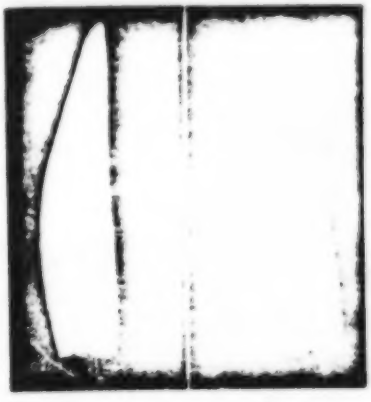


Figure 5. Ziphius cavirostris, Cuvier's Beaked Whale tooth; natural size (a) and x-ray (b). Approximately natural size.

a b

Figure 6. Globicephala scammoni, Pilot Whale, female; lateral aspect of tooth with abrasion notch (a); the x-ray (b) reveals the greatly reduced pulp cavity. Magnification 5:4.

A shiny tooth apex generally indicates the 7
presence of enamel, but a lusterless crown need not signify the absence of enamel. Thus, in Cuvier's Beaked Whale, the thin, dull enamel layer can only be seen microscopically. In addition, the enamel may be coated with cementum. A distinct circular striation of the root resulting from successive layers of dentine is found in killer whales, Cuvier's beaked whales, and pilot whales.

On all of the teeth, the dentinoenamel boundary --and therefore the presumed line of attachment of the gingiva-- lay between the upper third of the tooth and one-half of its length.

Evaluation of classification schemes (Cf. Table 1):

An attempt was made to classify the available material in three unified groups (a, b, and c). In every respect, a descending gradation was used; e.g., reduction

in size, number, or shape. The tabulation of the results provides an overview of the morphology of the teeth of certain Odontoceti. Also certain developmental trends are manifested. The values for body size and the number of teeth run in distinctly opposite directions among the Odontoceti. With increasing body size, the number of teeth decreases.

The length of individual teeth always approximates 8
one one-hundredth of the body length. Incidentally, this is true also in Man.

In all of the teeth, enamel and cementum were 9
found in very varied forms. The only exception was Berardius bairdii (pace YABLOKOW 1958). These teeth are characterized by the fact that the pulp cavity, which must have been taurodont earlier, is completely filled with a mass of collagen fibrils which can be readily cut (see p. 17). Apart from a thick layer of cementum around most of the tooth, only a 'crown-shaped' dentine tip actually qualifies as hard tissue.

Figure 7. Globicephala scammoni, Pilot Whale, male, lateral aspect (a) and x-ray (b) with immense pulp cavity; young tooth, 3:1.

Figure 8. Tursiops truncatus female, Bottle-nosed Dolphin. Lateral aspect of tooth (a) with occlusive surface of ground thin section as a strong sign of abrasion. X-ray (b) shows the tooth almost devoid of pulp, and filled with solid substance. 3:1.

Figure 9. Tursiops truncatus male, (a) lateral aspect of tooth, 2:1; (b) x-ray, natural size.

Figure 10. Stenella caeruleo-alba female, Blue-white Dolphin; (a) lateral aspect of tooth, 3:1; (b) x-ray, 2:1.

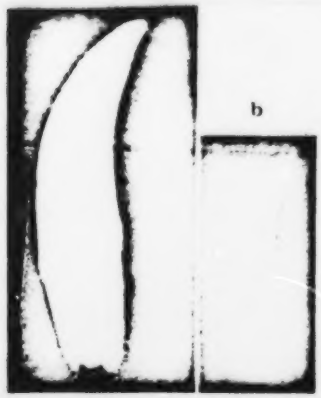


Figure 11. **Stenella caeruleo-alba** male, (a) tooth in lateral aspect, 4:1; (b) x-ray, 3:1.

Initially, the volume of the pulp cavity does not seem to follow any rule. Certainly on the basis of our specimens, of which the age was not known, Delphinus delphis and Phocaena phocaena could not be classified in YABLOKOW's first group with well developed pulp cavities.

Figure 12. Lagenorphynchus obliquidens male, Pacific White-sided Dolphin; (a) interior aspect of bisected tooth, 3:1; (b) x-rays of bisected tooth, 2:1.

However, generally the volume of the pulp cavity 10
depends primarily on the age of the animal, which should always be considered when making odontological comparisons of different species. In time, the often scanty enamel coating becomes abraded. Many Odontoceti lose part

or even all of their teeth as they age. This may also explain the partial inconsistency with YABLOKOW's (1958)

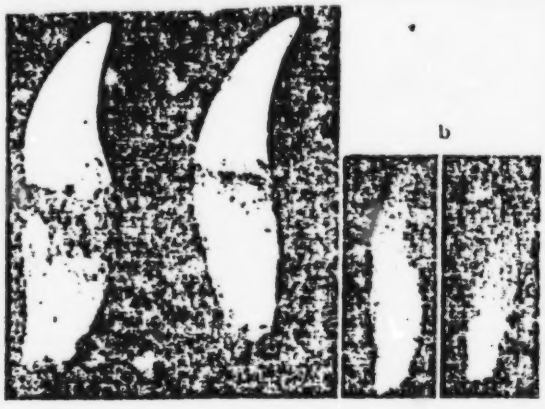


Figure 13. Delphinus delphis female, Common Dolphin; (a) tooth in lateral aspect, 4:1; (b) x-ray, 3:1, shows pulp densely packed to the end of the root.

findings. Hence, a systematic comparative investigation based on more extensive material of known age is all the more desirable.

Figure 14. Phocaena phocaena, Common Porpoise, lateral aspect of shovel-shaped tooth, 5:1; (b) x-ray, 3:1.

Histological section 11

According to the literature, the dental tissues are essentially like those of most mammmals. The prism

sheaths of the enamel are circular in cross section (SCHMIDT/KEIL 1958). According to FUKUHARA (1959), the enamel of the Pilot Whale Globicephala scammoni shows parallel lines as well as cross striation of the prisms. Between the parallel lines in the enamel there were two transverse striae crossing the prisms 3.2 µm apart; it is probable that the parallel lines reported by FUKUHARA were incremental lines. They were said to be 5.6 µm apart. In cetacean enamel the prisms trace a distinct S-shaped path (P. DE TERRA 1911). According to O. ABEL, vasodentine occurs in some toothed whales. PETER (1959) describes peritubular, or better, circumtubular zones around the dentinal tubules of Tursiops truncatus, with a mantle-like pattern of surrounding fibrils.

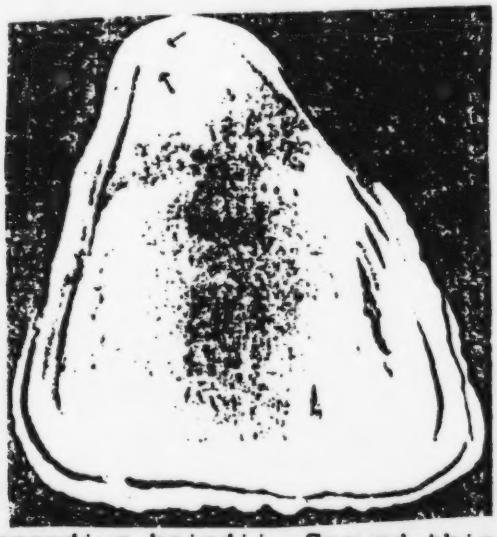

Figure 15. Berardius bairdii. Ground thin section through the middle of a tooth at its greatest width. Arrows indicate aggregated denticles between hard orthodentine or normodentine and the soft mass of fiber comprising the inner dentine which fills the pulp cavity (see also Figure 2, no. 2).

1. Structure of odontocetan teeth

Longitudinal sections, on which our investigations were primarily based, resembled those of human incisors or canines. The thickness of the enamel ranged from 40 to 320 µm. The enamel exhibits a coarse prism structure. From the dentinoenamel boundary to the surface, the prisms follow an S-shaped path, with slight deviations in individual species (see p. 20 f.). In the dentine there is almost always a distinct von Korff's zone where the fibers intersect the dentinoenamel boundary at an angle of $13^{o}$ to $55^{o}$. The enamel prisms originate as a direct continuation of the von Korff's dentinal fibrils. Usually a distinct interglobular dentine can be found underneath. The dentinal tubules are perpendicular to the dentinoenamel boundary. This produces a radial pattern of the tubules in the coronal region, which appears most distinctly in small teeth. The dentinal tubules cross the incremental lines at right angles. The thickness of the dentine increases as the pulp becomes thinner in the normal growth process of internal apposition. 12

About two-thirds of the tooth is covered with cementum, which may simply contact the enamel at the dentinoenamel boundary, but sometimes also forms a very considerable coating over the enamel, as in Ziphius cavirostris and Globicephala scammoni. Mere contact

Figure 16. Phocaena phocaena. Bundles of dentinal tubules in the vicinity of the pulp. Longitudinal section, 250:1.

between enamel and cementum was found in Orcinus orca and Tursiops truncatus (see Figure 27 and 28).

Teeth of Berardius bairdii are a special case: The enamel coating is completely absent, as is the pulp cavity (Figures 4 and 15). Except on the abraded tip, the tooth is completely surrounded with cementum, like a sperm-whale tooth.

A hard tissue composed of coarse fibrils is found at the base. Perhaps it represents an encapsulation formed by the surrounding tissue in reaction to the loss of the pulp. The shrinkage caused by dry storage made the differences between the tissues very distinct. The dentine appeared as a white cap, with the greater part of the 13
tooth composed of rather disorganized fibrous tissue. Large numbers of vascular interstices can be observed in this mass of fiber as well as in the dentine (Figure 22). Abundant denticular structures are present in the transitional area between the normally structured dentine and the disorganized fibrous tissue in the interior of the tooth (Figures 15, 20, and 21).

2. Fine structure of the dentine

The dentine of odontocetan teeth is essentially similar to the normal von Ebner's dentine of most Mammals. Only cynodont and lithodont teeth show peculiarities of fine structure (e.g., Berardius bairdii and Globicephala scammoni).

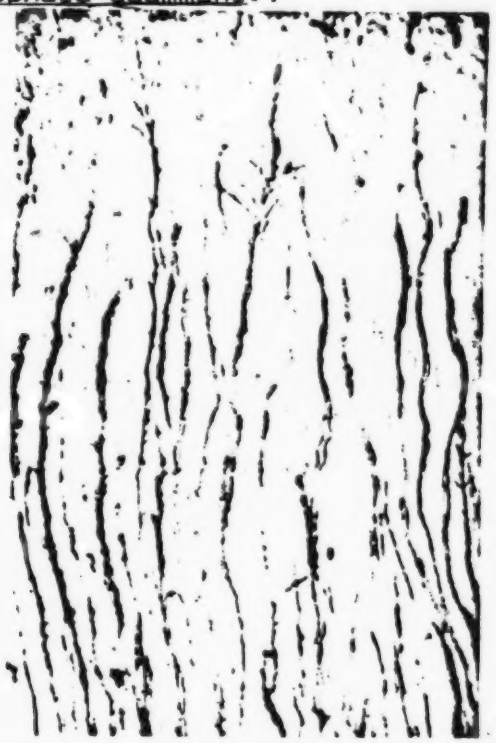

Figure 17. Ziphius cavirostris. Branching of individual dentinal tubules. Longitudinal ground thin section. 250:1.

The orientation of the dentinal tubules is uni- 14
formly radial, but a closer view reveals coiling with multiple branching (Figure 17). In Phocaena phocaena, several tubules always start together from the pulp at fixed intervals (Figure 16). Cross-cut dentinal tubules appear with a phase contrast microscope as bright shining

spots. In polarized light, we see negatively signed darkened crosses around cross-cut tubules (representing the surrounding network of collagen fibrils). The intensity and the sign of the birefringence are determined mainly by bundles of collagen fibrils.

Figure 18. Orcinus orca. Arcaded structure of dentine in longitudinal section; polars crossed diagonally, 250:1.

The course of the collagen fibrils appears more distinctly on the boundaries of the dentinal growth layers, which record the rhythm of growth. As external limits of a given stage of increment, the growth layers end at the surface of the dentine. The first clear incremental line expires in the area of the enamel-cementum boundary.

In normal transmitted light, ground thin sections of odontocetan teeth exhibit two particularly striking features: 1. the granular layer below the surface of the

dentine, and 2. the zone of (inter)globular dentine (Figure 19). Interglobular spaces surround the individual globuli. Similar globular structures can be found in other sections in areas near the pulp, where they form a globular termination on thin-ending parts of the section. Closer to the center of the dentine, globular calcifications may form a particular area reminiscent of an alveolar pattern. In the rest of the dentine, the pattern of incompletely formed globuli-- i.e., rotatory parabolic calcospherites, also known as dentinal arcades -- is fairly distinct and widespread in most sections (Figure 18). While the arcades in an untreated ground thin section are manifested in polarized light only by compensatory phenomena of birefringence (collagen 'positive' and apatite 'negative'), their calcospheritic character can be demonstrated by de-collagenation followed by imbibition (e.g., with quinoline), through the sole (negative) birefringence of the apatite crystals with the appearance of a polarization cross (for details see SCHMIDT/KEIL 1958, p. 63 ff.). The diameter of the arcades was measured at their widest cross section (viz., at the base) in all species except Berardius bairdii, Ziphius cavirostris, Stenella caeruleo-alba, and Phocaena phocaena. It ranged from 10 to 40 µm. In specimens in which arcades as well as globuli occurred, it was found that the diameter of both forms of calcification was of the same order of magnitude. This indicates that both

15

forms originated from the same principle of formation. Arcades are modified globular structures, but typical for almost all Mammals which have been studied in this connection so far.

Figure 19. Tursiops truncatus. Longitudinal section from a tooth, with interglobular dentine. 250:1.

Phase-contrast pictures of dentine present the same type of alveolar structure as in Figure 18. In favorable cases, the polarization crosses could be discerned also in untreated ground thin sections, as has been shown occasionally also for human dentine (A. KEIL 1934). Viewed more closely, the path of the incremental lines is undulating, probably because of the influence of the partly globular mineralization. The partly globular, partly linear boundary of the spherites is as expected according to Popoff's laws. The polarizing microscope also reveals other types of calcium salt depositions. While mineralization along the collagen fibrils does not show because of the weakness of the birefringence, the crystalites along the dentinal tubules are clearly

manifested. In closing, it can be stated with regard to the types of calcification in the dentine of odontocetan teeth that there are basically two different types:

1. Calcification bound to organic ground structures
    a) along the collagen fibrils
    b) along the dentinal tubules
2. Spheritic calcification
    a) complete: globuli
    b) incomplete: arcades (semi-globuli)

Figure 20. Berardius bairdii. Marginal zone of the dentine, with the transitional area from normodentine (through denticular 'pearls') to the transformed inner dentine (see Figure 15); ground thin section, 4:1.

Von Korff's dentine, which is approximately equivalent to 'mantle dentine', was found in all of the

teeth investigated. The network of fibrils radiated onto the surface of the dentine at an acute angle from the apical end (at the root) to the coronal end (towards the crown). This layer seems largely to correspond with what is known as the 'granular layer'. In phase contrast, the von Korff's dentine appears as a brightly shining zone. The globuli in the von Korff's dentine are smaller than in the von Ebner's dentine which is next inside. In the surface layers, this leads to the smallest globuli in the Tomes' granular layer.

In suitable specimens with cross-cut dentinal tubules (in areas close to the pulp) the tubules could be counted with a counting grid at a magnification of 250:1 (the area covered then equals a square with sides measuring 25 $\mu$m). This procedure yielded the following average values for an area of 25 $\mu m^2$:

| species | dentinal tubules |
|---|---|
| Delphinus delphis | 7 |
| Phocaena phocaena | 8 |
| Tursiops truncatus | 11 |
| Stenella caeruleo-alba | 12 |

Berardius bairdii and Globicephala scammoni show 17
a common trend: In one, there is no longer any pulp cavity; in the other, a reduction of the pulp cavity is in progress. This is indicated by the many spaces in the dentine close to the pulp, which contained cells in the vital state. Presumably this area represents an

especially wide fringe of dentine-forming cells, but they form irregularly structured dentine. The pulpal wall of Globicephala scammoni exhibits roundish structures similar to those found crowded along the inner margin of the dentinal cap in Berardius bairdii. However, the latter structures are free of cells, whereas they contain cells in Globicephala scammoni. In Berardius bairdii these structures are designated as denticles, and they are connected with filling the pulp cavity. Here they are especially numerous, and show a negative extinction cross in polarized light. Their structure is concentrically layered, and in addition, it also shows a radial pattern. The latter is due to the transverse striation of the 18
individual collagen elements (Figure 20 and 21). In Berardius bairdii, both the pulp cavity, which is filled with collagen, and the dentine, which is present only at the apex of the tooth, contain abundant spaces from former vascular interstices (Figure 22). Unfortunately the conditions in which this tissue rich in blood vessels is formed and walled in with a thick layer of cementum can hardly be further clarified, because vital material is not readily accessible[1].

[1] Occasionally similar behaviour has been found also in other Mammals. EIDMANN found that the pulp cavities of adult Elk (Alces alces L.) were usually completely filled with secondary dentine. --Control of this process in Man would open the possibility of a 'physiological root filling' as a therapeutic goal. This desirable situation has also been described in Man as a spontaneous occurrence (HARNDT, 1960). See the addendum on p. 32.

3. Fine structure of the enamel

Enamel occurred on most of the investigated teeth as a constant, macroscopically visible layer. Exceptions were the teeth of Berardius bairdii with no enamel, sperm whale teeth as a rule, and the microscopic enamel layer of Ziphius cavirostris, which is only 40 µm thick. The precise thickness of the enamel layer (expressed in µm) for the individual species under study was as follows:

| | |
|---|---|
| *Orcinus orca* | 200 |
| *Berardius bairdii* | (nil) |
| *Ziphius cavirostris* | 40 |
| *Tursiops truncatus* ♀ | 224 |
| *Tursiops truncatus* ♂ | 320 |
| *Globicephala scammoni* ♀ | 300 |
| *Globicephala scammoni* ♂ | 280 |
| *Stenella caeruleo-alba* ♀ | 117 |
| *Lagenorhynchus obliquidens* | 160 |
| *Stenella caeruleo-alba* ♂ | 144 |
| *Delphinus delphis* ♀ | 120 |
| *Phocaena phocaena* | 165 |
| corr'spg values in Homo | 2140 |
| and *Cercopithecus aethiops pygerythrus* (Guenon) | 640 |

The thickness of the enamel was always measured at the thickest part of the ground thin section, usually in the area of the tooth apex. Odontoceti with very few teeth, such as Berardius bairdii with 4 to 8, had no enamel, and Ziphius cavirostris with 2 teeth retained only a 'rudimentary' enamel layer. Globicephala scammoni and Tursiops truncatus showed the thickest enamel, measuring as much as over 300 µm. The enamel layer of the other species varied between 100 µm and 200 µm. There was no discernible relation between enamel thickness and the size of the teeth.

Figure 21. Berardius bairdii. Magnified portion of Figure 20; a) normal transmitted light, b) crossed polars. Cruciform extinction area represents concentric layering of denticle. 35:1.

Our description of the fine structural features 20
of the tooth enamel of the investigated Odontoceti is based primarily on the teeth of Orcinus orca, Globicephala scammoni and Tursiops truncatus. As the enamel layer becomes thinner, the structure becomes more homogeneous, or individual structural features are obscured. Thus, no

histological differentiation can be seen with an optical microscope in the 40 µm enamel layer of Ziphius cavirostris. Negative birefringence to the layer normal shows that the mineral portion of the enamel has the same orientation as in all other species. The enamel of all of the odontocetan teeth investigated is interspersed with numerous cracks and tears. Some of these may be due to the exsiccation, or artefacts of the grinding process; others must be present also *in vivo*.

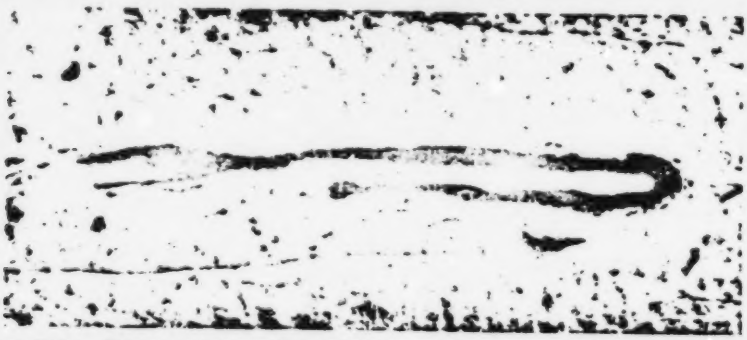

Figure 22. Berardius bairdii. Vascular loop in the outer dentine, 500 :1. Phase contrast photomicrograph.

Very small cracks extending only a short distance inward from the dentinoenamel boundary are known as 'enamel tufts' (Schmelzbueschel) (Figure 23, cf. figure 182 in SCHMIDT/KEIL 1958). Enamel cracks extend through the entire enamel and may form a depression in the surface (Figure 23). It is these cracks that are probably not artefacts, but due to structural abnormalities. They owe their microscopic appearance to reflection from pores containing air.

The path of the enamel prisms is uniformly arcuate. In Phocaena phocaena, the prisms are more

perpendicular to the dentinoenamel boundary. The individual prisms are crudely joined together, so that interprismatic substance approximately equal to their own width remains between them. The birefringence of the prisms is very strong. In the extinction positions of the prisms, the interprismatic spaces are brightly visible (Figure 24). 21

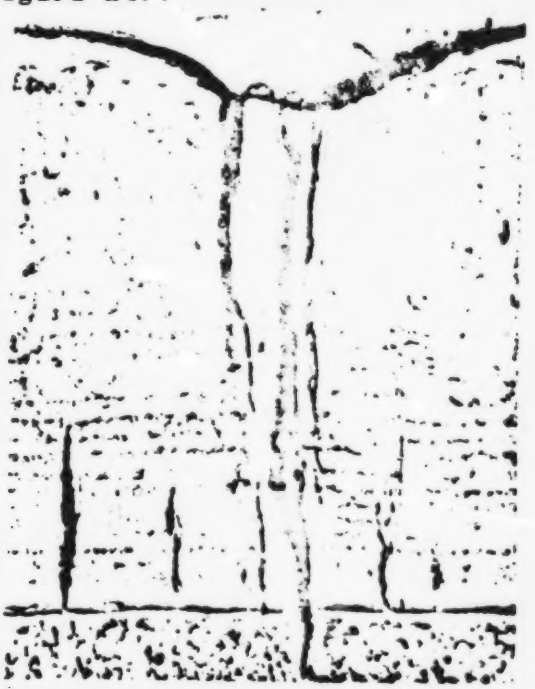

Figure 23. Orcinus orca. Cross section through the enamel-bearing acral end of a tooth. A typical depression of the enamel surface, with enamel lamella (crack?) and enamel tufts in the basal third of the enamel. 250:1.

All species investigated exhibited cross striation of the prisms. Because of the uniform orientation of the prisms, the cross striation takes on the appearance of an undulating parallel striation traversing the enamel (Figure 24), which occurs chiefly in the superficial regions of the enamel and also passes through

those zones with positive birefringence. In those odontocetan teeth with a thick enamel layer, the striation of Retzius is distinctly visible. It traverses the entire width of thin-ending enamel (Figure 25), or occurs in the basal portions of the thicker layers (Figure 24), starting from the dentinoenamel boundary at an acute

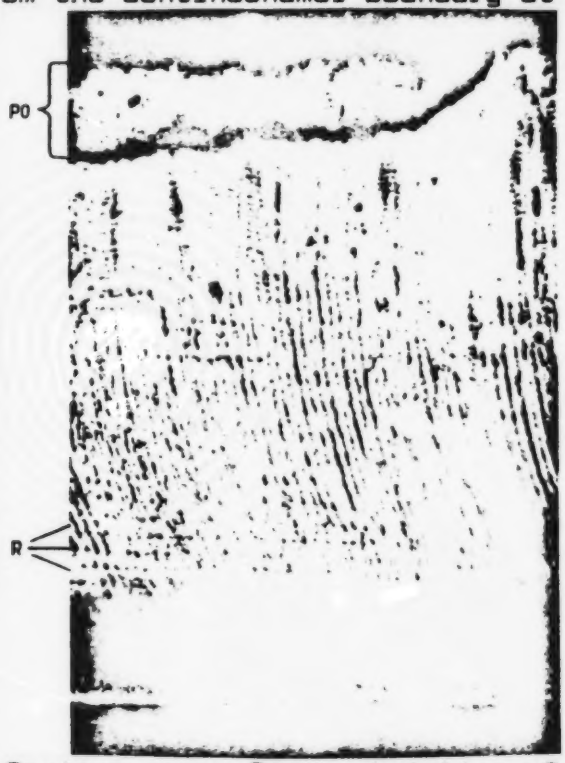


Figure 24. Orcinus orca. Cross striation of prisms more in the younger, outer enamel; more distinct striation of Retzius (R) in the older, inner portion. Distinct 'positive' zones (PZ). Longitudinal ground thin section; 250:1.

angle and extending coronad to the surface of the enamel. The angle at which the striae of Retzius intersect the surface ranges from $5^{o}$ to $10^{o}$. The outer regions of the enamel, where parallel striation can be found, show only very indistinctly outlined prisms,

whereas the contours of the prisms in the basal portion of the enamel with the striation of Retzius are distinct (Figure 24). The outer margins of the prisms are not linear, but constricted at certain intervals. Generally the enamel was negatively birefringent to the direction of the prisms. However, in all species investigated with one exception (Ziphius cavirostris), positively birefringent zones were found in the enamel, usually in the superficial regions (Figure 26). These were sharply differentiated from the negatively birefringent part of the enamel, with jagged contours. The detailed study of these zones was performed by means of imbibition, which with its changing optics indicates a certain type of fine structure. Hydrophilic and lipophilic infiltration ~~imbibition~~ media were used in two separate series, with the following refractive indices: xylol 1.49, ethyl alcohol 1.36 and water 1.33, Thoulet's solutions 1.43, 1.54, 1.62 and 1.72, and air (1.00). The thin, very rudimentary enamel layer of Ziphius cavirostris was uniformly negatively birefringent in all media, i.e., it was not affected by these media, and no optical changes were observed even in air. Tursiops truncatus shows positively birefringent zones only in air. Ground thin sections of the enamel of all other species had uniformly positively birefringent areas after infiltration ~~imbibition~~ with xylol, alcohol and air (Figure 26); the areas were largest with air. Also aqueous infiltration ~~imbibition~~ media made the enamel uniformly

23

negatively birefringent, with one exception (Phocaena phocaena) (Figure 26). Usually the penetration of the medium into the thin section was already finished in 24
a few minutes.

Figure 25. Orcinus orca. Striation of Retzius in the enamel; a) incisal/acral portion of enamel cap, b) cervical ending of enamel. Polars crossed diagonally. Longitudinal ground thin section; 100:1.

infiltration

Occasionally ~~imbibition~~ with Thoulet's solution took a long time (2-3 hours) and had to be done in a moist chamber in an incubator. In some species, positively birefringent zones reappeared after imbibition with Thoulet's solution (refractive index 1.72). The enamel of Phocaena phocaena (no. 12) showed a different behaviour; 25
in this case the positively birefringent zones became progressively smaller from water to Thoulet's solutions 1.43 and 1.54, but disappeared entirely only at a refractive index of 1.62, and were positive again at 1.72.

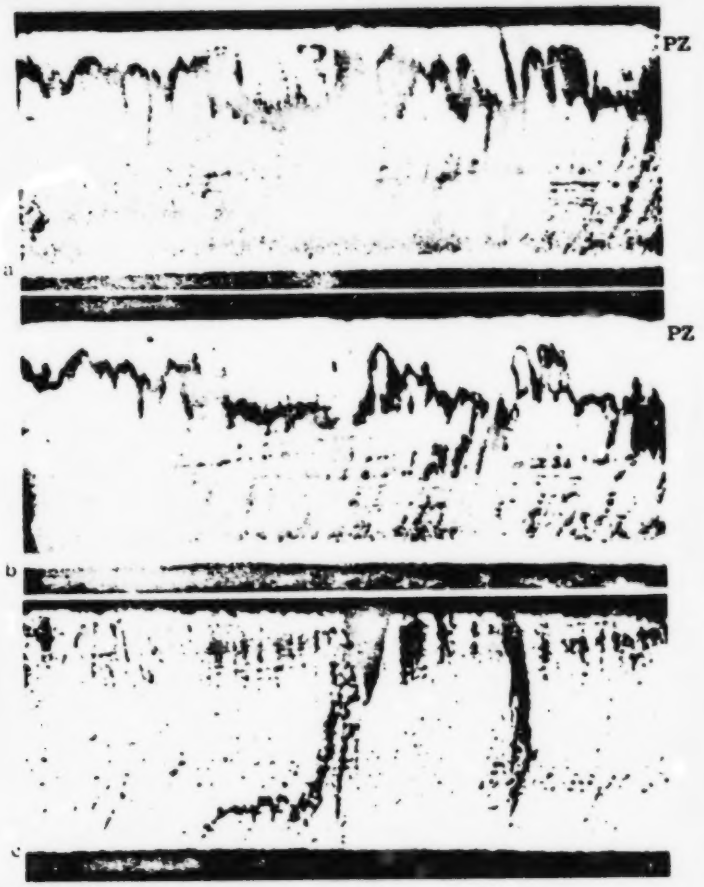


Figure 26. Orcinus orca. 'Positive' outer zones (PZ) in otherwise 'negative' enamel; a) in ethyl alcohol, b) in xylol, c) in water. Polars crossed diagonally, 100:1.

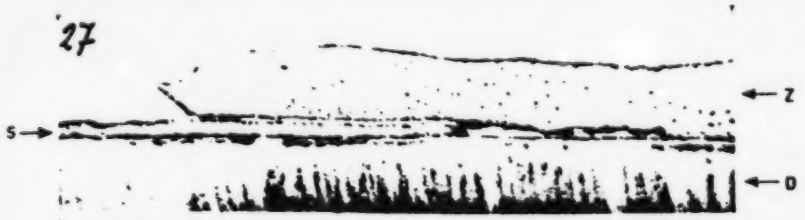


Figure 27. Ziphius cavirostris. Thin, but highly mineralized enamel layer (S) with widely overlapping cementum (Z). D= dentine. --35:1.

In summary, a comparison of the results of infiltration with different media of the same refractive index shows a difference between lipophilic and hydrophilic media. We should have expected that alcohol

(1.36) would have the same effect as water (1.33) and that xylol (1.49) would act like Thoulet's solutions (1.43 or 1.54), but this is not the case. Despite equal or similar refractive indices, positively birefringent zones appear in lipophilic media which disappear in hydrophilic media. A similar pattern was observed also in other enamel by SONI and BRUDEVOLD (1959) and GWINNETT (1965). They explained these positively birefringent zones as an artefact from the dehydrating action of the alcohol medium and subsequent entry of air into the pores thus created. Therefore water and aqueous solutions give the most reliable results concerning the submicroscopic porosity of tooth enamel.

Hence in the enamel studied in the present investigation, the positive birefringence is based on the enclosure of air-- a medium with a refractive index sufficiently different from the mean refractive index of the enamel (1.62)-- in submicroscopic pores, and should be designated as form birefringence, which, however (with the single exception of Phocaena phocaena) is already overcompensated in water by the birefringence of the enamel itself.

The imbibition of the enamel under study allows the following conclusions: Positively birefringent areas produce molecular-sievelike porosities in the enamel. When the medium used is water (index 1.33) or Thoulet's solutions

(1.43 to 1.72), the sign of the birefringence is almost uniformly negative.

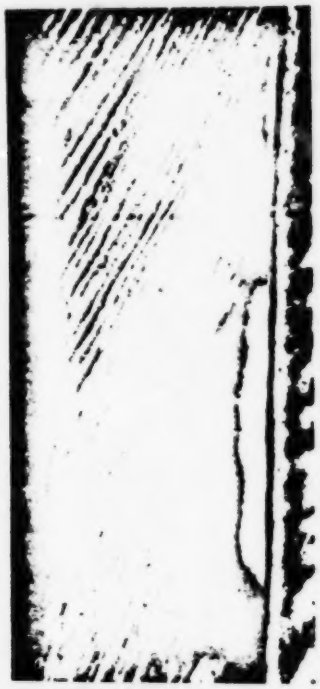

Figure 28. Ziphius cavirostris. Thick layer of cementum over thin enamel. Layering revealed between crossed polars, 100:1.

Air was the only imbibition medium with a refractive index sufficiently different from that of the mineral substance of the enamel to be able to overcompensate the negative birefringence of the enamel itself with positive form birefringence. HARDERS-STEINHAEUSER (1938) showed in a study of the imbibition behaviour of newly formed human enamel at different stages of maturation that such behaviour is associated with a high degree of mineralization. W. KALB (1967) confirmed similar results in his study of the process of mineralization of the enamel in Hippopotamus. By analogy, we may

infer a high level of mineralization in the enamel of the odontocetan teeth investigated. Only the enamel of Phocaena phocaena shows a uniformly negative birefringence after imbibition with Thoulet's solution 1.62, and therefore appears to have a lower degree of mineralization (n.b.: at the end of 'maturation', i.e., in broken teeth). 27

Histological comparison with Primate teeth

In Primates, the enamel is composed of thin, elongated prisms. Diazones and parazones, Hunter/Schreger's bands arise from the helical shape of the prisms.

We measured the thickness of the enamel as 2140 µm in Man and 640 µm in Cercopithecus (measured at the tubercles), or respectively ten and two times the maximum thickness of odontocete enamel.

The structural pattern exhibits certain differences. The 'prisms' of odontocetan teeth seem crudely structured and indistinctly bounded, and extend almost straight from the dentinoenamel boundary to the surface of the enamel. The striae of Retzius meet the enamel surface at a wider angle in Primates than in Odontoceti (over $30^{o}$ in Man, $10^{o}$ - $20^{o}$ in apes, but less than $10^{o}$ in toothed whales hitherto investigated). The striae in toothed-whale enamel are also much fewer in number. Thus, compared to primate enamel, the enamel of the toothed whales appears thinner, and more smoothly extended along

the axis of the tooth. Moreover, primate enamel in the mature, well mineralized state is uniformly negatively birefringent to the length of the prisms, whereas all of the odontocete teeth which we investigated, if they have a mantle of enamel, exhibit positively birefringent areas in the enamel, or areas of hypocalcification, as a normal feature.

The dentine of primates exhibits the same forms of mineralization as that of Odontoceti. The globuli in some Odontoceti are more numerous and more distinct than in primate dentine. With respect to the dentinal arcades, two differences are especially striking: 1. Their diameter measures between 10 and 40 $\mu$m in the odontocetan teeth, while the corresponding values hitherto reported for the teeth of Man and apes are 100 $\mu$m or more. However, in addition to these 'macro-arcades', there are also many 'micro-arcades' (in the same order of magnitude as those of odontocete teeth) in the dentine of primate teeth. 2. Whereas the arcades in the toothed whales are evenly distributed throughout the dentine without striking variations of size, in the dentine of primate teeth the 'macro-arcades' occur in the outer regions of von Ebner's dentine, while the 'micro-arcades' occur more in dentine close to the pulp.

Discussion of the findings 28

The shape of Recent whale teeth represents the basic haplodont type. The teeth of Phocaena phocaena appear almost like small human canines, and still show most clearly a 'crown' and a 'root'. In all other species, the external shape does not permit any exact differentiation; these teeth have been reduced to a simple conical shape with subcircular cross sections at all levels. The pulp cavity evidently becomes progressively narrower with increasing age.

HILZHEIMER's (1913) division of coelodont teeth (with persistent pulp) and pleodont teeth (solid) was subdivided into taurodont (large pulp), cynodont (small pulp), and lithodont (pleodont, solid).

In small teeth like those of dolphins and porpoises, the formation of secondary dentine to fill out the pulp proceeds without important structural changes. In the larger teeth investigated (Berardius bairdii, Globicephala scammoni), the disappearance of the pulp is accompanied by the formation of numerous adherent denticles. This corresponds also with the findings for sperm whales (KEIL 1962).

PURTZ (1964) and STIER (1965) give detailed descriptions of denticles enclosed in sperm-whale teeth. These phenomena are definitely age-related; also in human teeth, we can observe a transition from juvenile 'taurodonty' to adult 'cynodonty' (of course, 'lithodonty', or

solid replacement of the entire pulp, is very rare). Generally, then, the pulp becomes progressively narrower. According to the above remarks, also the opposite finding in Delphinus delphinus and Phocaena phocaena should be interpreted in opposition to YABLOKOW's classification (see p. 2 ff.). At the same time, another error of YABLOKOW may be corrected here: Orcinus orca, the Killer Whale, is placed in the group without enamel, and Berardius bairdii, Baird's Whale, is placed in the group with enamel. However, we found the opposite in the teeth which we examined: Among Odontoceti, only Berardius bairdii had teeth without enamel (regarding the Sperm Whale, see above, p. 1).

In longitudinal ground thin sections, most odontocetan teeth resemble human incisors or canines. The dentine shows greater resemblance morphologically and histologically to human dentine, for example, than does the enamel. This applies also to structural details which are characteristic of mammalian dentine. Mantle dentine (von Korff's dentine) and von Ebner's dentine can be readily differentiated. Similarly, numerous incremental lines can be found in the dentine of Odontoceti. Also the interrelations of particular structural elements, such as the orientation of the dentinal tubules to the incremental lines, correspond to the general plan of mammalian dentine. Interglobular dentine is a sign of inhomogeneous calcification. Dentinal arcades were confirmed as a

regular structural feature of the dentine of the odontocetan teeth investigated. They are of a different order of magnitude compared to the arcades of primate teeth ('macro-arcades' 100 µm or more, 'micro-arcades' up to 40 µm).

The enamel of Odontoceti shows prisms with cross striation and striation of Retzius. However, morphologically and structurally it must be described as reduced, at least compared to human tooth enamel, because of the following features: 1. low thickness, 2. irregular 'prism' structure, and 3. permanent zones of hypocalcification ('positive' zones) in all areas of the enamel. In view of these three factors, the enamel of Odontoceti can be designated as deficient, and in the process of reduction. The enamel layer of Ziphius cavirostris, now only 40 µm thick, can even be considered 'rudimentary', especially since this designation is confirmed by incomplete mineralization in the form of positively birefringent zones in the enamel. In human enamel, such zones, as permanent growth abnormalities, are exceptional (see also RIPA et al. 1966 concerning superficial parallel hypocalcifications in Man); in Odontoceti, they are the rule.

Summary

Individual teeth of the following toothed whales were subjected to comparative anatomical and histological investigations:

*Orcinus orca, Berardius bairdii, Ziphius cavirostris, Globicephala scammoni* (♂ and ♀), *Tursiops truncatus* (♂ and ♀), *Stenella caeruleo-alba* (♂ and ♀), *Lagenorhynchus obliquidens* ♂, *Delphinus delphis* ♀, *Phocaena phocaena.*

1. Formal deviations from the haplodont ground plan are lateral arcuate divergences (the most frequent type), corkscrew-shaped, spatulate, and triangular forms.
2. The length of the teeth (ranging from 16 cm to 0.9 cm) is equal to approximately 1/100 of the body length of the species in question.
3. The size of the pulp cavity makes it possible to differentiate taurodont, cynodont, and lithodont (pleodont) teeth:

Taurodont: *Orcinus orca, Globicephala scammoni* ♂, *Lagenorhynchus obliquidens* ♂, *Stenella caeruleo-alba* ♂. Cynodont: *Ziphius cavirostris, Tursiops truncatus* ♀, *Stenella caeruleo-alba* ♀. Lithodont (pleodont): *Globicephala scammoni* ♀, *Tursiops truncatus* ♂, *Delphinus delphis, Phocaena phocaena, Physeter macrocephalus.*

4. Histologically, the dentine of the teeth investigated resembles that of other Mammals. In all of these teeth, the von Korff's dentine is distinct; incremental lines are present as a rule. The Tomes' granular layer is located in the outer region of the von Korff's dentine, and evidently consists of very small globular calcifications.

5. The dentine of all toothed whales investigated normally exhibits semi-spherites ('arcades') and spherites ('globuli') as mineralization structures.

6. Different degrees of obliteration of the pulp cavity were found, often in association with massive formation of denticles.

7. Vascular loops were enclosed in the dentine of Berardius bairdii, as well as in the easily cut mass of collagen replacing the obliterated pulp of lithodont (pleodont) teeth.

8. All of the teeth investigated except those of Berardius bairdii have enamel layers with a thickness of 40 to 320 µm.

9. The enamel is composed of crudely structured 'prisms' which follow an S-shaped path (with minor deviations) from the dentine to the surface of the enamel. The 'prisms' exhibit cross striae which are revealed by imbibition with quinoline.

10. In all regions (superficial, medial, and basal) the enamel may exhibit hypocalcifications recognizable as positively birefringent zones (in air 1.00, alcohol 1.36, and xylol 1.49). After ~~imbibition~~ infiltration with water (1.33) and Thoulet's solutions (1.43 - 1.72), the enamel is usually uniformly negatively birefringent; a sievelike system of submicroscopic pores is present, signifying that mineralization must be either incomplete or arrested at an immature stage.

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1. Teeth, in Manual of natural sciences, second edition, vol. 10

2. Dental tissue and periodontium.--Manual of primatology, III, Part 2... Basle and New York

3. To the knowledge of the formation of replacement dentine in Cervidae

4. Studies of cervid teeth. II. Development of temporary canines in Cervus elaphus L. (French summary)

5. The hardening of tooth enamel, based on polarizing microscopic investigations

6. Filling of the root canal with the body's own hard tissue

7. 'Dentition', in: Digestive tract of Reptiles

8. New studies on the progressive mineralization and hardening of maturing dental enamel, as seen in Hippopotamus canine teeth (dissertation)

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11. Outline of odontology. General and comparative study of teeth as organology. Second edition

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15. Contribution to the study of spherolith formations ...Sect. IV

16. ...second edition (chapter 23...)

17. Concerning the histology of the pulp of a sperm-whale tooth (dissertation)

18. Giants of the Sea. A biology of Whales and Dolphins

19. Healthy and diseased dental tissue of Man and Vertebrates under a polarizing microscope. Munich

20. Histological and histochemical investigations of the pulp of a sperm-whale tooth fractured in vivo. (dissertation)

21. Comparative anatomy of human dentition and vertebrate teeth

22. Mammalia. Vol. 2

Addendum in proof

Two more very rare cases of human dentinal dysplasia with solid filling of the pulp cavity are described by P. BRUSZT (1969, Bull. Group. Int. Rech. Sc. Stomat., 12, 107-109) as a hereditary abnormality in all teeth (of father and daughter), in which the pulp cavity was 'filled with a hard substance composed of concentric lamellae'. This obliteration already began before the teeth erupted and continued as they grew. It was not related to any general disease (unlike, e.g., dentino-

genesis imperfecta, which also is hereditary, and runs closely parallel with osteogenesis imperfecta). Hitherto such rare cases of generalized dentinal 'calcinosis' have been described only in England, the United States, Germany, and Hungary. Bruszt recalls the regular massive filling of the pulp cavity of the teeth of the fossil fish Glyptolepis (reproduced in KEIL 1966). (A.K.)

Author's address:

Professor Dr. Dr. Albert Keil [ ...University Dental Institute]
Zahnärztliches Institut der Universität
63 Gießen, Friedrichstraße 28

Dr. Heinrich von Nolting
632 Alsfeld (Oberhessen)
Am Lieden 3

(Federal Republic of Germany)